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The earliest known restoration of a pterosaur and the philosophical origins of Cuvier's *Ossemens Fossiles*

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Abstract

The oldest known restoration of a pterosaur, sent by Professor Jean Hermann of Strasbourg to Georges Cuvier in Paris in 1800, was never published. But it has been found, along with many of Cuvier's important papers and letters, in the archives of the central library of the National Museum of Natural History in Paris. The sketch is unusual in many respects because Hermann interpreted the animal as a better possible intermediate between birds and quadrupeds than bats would be. Although Hermann's reconstruction had little influence on Cuvier, it drew the latter's attention to Collini's 1784 paper, the first ever on these animals, which Cuvier would later name *ptéro-dactyles* without ever seeing the original specimens. Collini's drawing immediately convinced Cuvier that the mysterious animals were reptiles, and that they could fly. Cuvier's expertise with the patterns of comparative anatomy allowed him to correct many interpretations of other workers, who visualized pterosaurs as mammals, birds, bats, amphibious or marine animals, or as intermediates between different groups. These somewhat tentative, complex concepts of the structures and 'affinities' of prehistoric life reflect the fluidity of pre-evolutionary, horizontal 'arrangements' in contrast to later evolutionary, vertical classifications based on ideas about phylogeny. But Collini's paper also immediately provided a strong theoretical underpinning for Cuvier's prospectus for his great work, *Ossemens Fossiles des Quadrupèdes*. Shortly after reading Collini's paper, Cuvier developed the introduction to his 1800 prospectus, incorporating many of Collini's rhetorical strategies with his own views. These same ideas also became important in Cuvier's *Discours préliminaire* to the *Ossemens Fossiles*, his most renowned philosophical work. ***To cite this article: P. Taquet, K. Padian, C. R. Palevol 3 (2004).***

Résumé

La plus ancienne reconstitution d'un ptérosaure et les origines philosophiques des *Ossemens Fossiles* de Cuvier. La plus ancienne reconstitution d'un ptérosaure, envoyée par le professeur Jean Hermann de Strasbourg à Georges Cuvier à Paris en 1800, n'a jamais été publiée. Elle est cependant présente, avec des documents importants et des lettres dans les archives de la Bibliothèque centrale du Muséum national d'histoire naturelle, à Paris. Le dessin est assez insolite à bien des égards, car Hermann a interprété l'animal comme le meilleur intermédiaire possible entre les oiseaux et les quadrupèdes tels que les

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chauves-souris. Bien que la reconstitution d'Hermann n'ait eu que peu d'influence sur Cuvier, elle a attiré l'attention de ce dernier sur l'article de Collini de 1784, le premier qui ait traité de ces animaux que Cuvier devait nommer plus tard « ptéro-dactyles », sans même avoir vu le spécimen original. Le dessin de Collini convainquit immédiatement Cuvier que ces animaux mystérieux étaient des Reptiles et qu'ils pouvaient voler. L'expertise de Cuvier avec les modèles tirés de l'anatomie comparée lui permit de corriger de nombreuses interprétations des autres auteurs qui ont représenté les ptérosaures comme des mammifères, des oiseaux, des chauves-souris, comme des animaux amphibiens ou marins, intermédiaires entre différents groupes. Ces premiers essais complexes des structures et des « affinités » de la vie préhistorique reflètent la fluidité des « arrangements » pré-évolutifs, horizontaux, qui contrastent avec les classifications évolutives verticales plus tardives, basées sur des idées tirées de la phylogénie. Mais l'article de Collini fournit aussi immédiatement une solide assise théorique au prospectus de Cuvier pour son grand ouvrage sur les *Ossemens Fossiles de Quadrupèdes*. Cuvier, très rapidement après la lecture de l'article de Collini, développa l'introduction de son prospectus de 1800 en incorporant à ses propres vues bon nombre des stratégies rhétoriques de Collini. Les mêmes idées occupent une place importante dans le *Discours préliminaire* aux *Ossemens Fossiles* de Cuvier, son œuvre philosophique la plus célèbre. ***Pour citer cet article : P. Taquet, K. Padian, C. R. Palevol 3 (2004).***

Keywords: Pterosauria; Pterodactylidae; Upper Jurassic; Germany; History of Paleontology

Mots clés : Pterosauria ; Pterodactylidae ; Jurassique supérieur ; Allemagne ; Histoire de la Paléontologie

Version française abrégée

1. Introduction

Les ptérosaures font partie des organismes les plus étranges que l'on puisse trouver dans les archives du passé. Depuis leur découverte, leur corps, leurs ailes, leur vol, leur posture et leur revêtement dermique ont été reconstitués de différentes manières [13,21,38].

Le premier ptérosaure complet a été trouvé dans les calcaires marins du Jurassique supérieur de Bavière [4,8,9,19,20,28,29]. En 1925, le paléontologue O. Abel a publié les dessins des premières reconstitutions de ptérosaures, dont la plus ancienne était celle, pensait-il, de Johannes Wagler [36]. En réalité, il y avait une image plus ancienne [21], due à Samuel Theodor von Soemmerring [29], qui présentait le ptérodactyle sous la forme d'une chauve-souris. Cependant, Cuvier, dans ses publications de 1809, puis de 1812, avait signalé l'existence d'une reconstitution due à son ami le professeur Jean Hermann de Strasbourg, sans jamais la publier.

Le but de cette note est de présenter les dessins réalisés par Hermann, de donner quelques précisions sur les débuts de l'interprétation des ptérosaures et de montrer également quelle fut l'influence de l'envoi de Hermann sur Cuvier.

2. La reconstitution d'Hermann

En mars 1800, Cuvier reçut une lettre de Jean Hermann de Strasbourg ; Cuvier avait décidé en 1798 d'écrire un large traité sur tous les vertébrés fossiles connus [6]. C'est la raison pour laquelle son ami Hermann lui signala l'existence d'un article écrit par Collini [4] dans les *Mémoires de l'Académie* de Mannheim, dans lequel se trouvait la description d'un animal très singulier, qui avait dû former, selon lui, une espèce intermédiaire entre les mammifères et les oiseaux. Hermann aurait voulu publier un mémoire sur cette pièce, mais il n'en eut pas le courage.

Ce squelette singulier était celui du premier ptérosaure jamais décrit, celui que Cuvier nommera en 1809, « ptéro-dactyle » : la pièce avait été décrite en 1784 par Collini, un florentin qui avait été le secrétaire de Voltaire, et Hermann attira l'attention de Cuvier sur le texte de Collini. Les deux dessins d'Hermann qui accompagnaient la lettre montrent l'animal « revêtu de son poil », bien que ce ne soit pas le cas de la plupart des ptérosaures connus aujourd'hui ; les dessins montrent en tout cas qu'Hermann avait parfaitement reconnu qu'il s'agissait d'un animal volant. Il reconstitua celui-ci comme s'il était proche des dermaptères et des chauves-souris, tout en courbant les os du doigt supportant l'aile (Figs. 1 et 2).

3. Cuvier et le ptérodactyle

Cuvier écrivit en Allemagne au baron Moll pour retrouver le spécimen, mais ce dernier ne put retrouver le fossile qui fut en fait étudié par Samuel Theodor von Soemmerring. Soemmerring lut en 1811 l'article publié par Cuvier en 1809 [8] et se désola de voir que Cuvier plaçait ce fossile parmi les reptiles, alors qu'il était d'avis de le placer parmi les mammifères. Cuvier donnera la description du ptérodactyle uniquement d'après la description de Collini; il obtint de Soemmerring un moulage du spécimen en 1818.

Collini, bien que n'étant pas anatomiste, avait cependant une excellente éducation et une fine perception des choses, et sa description est élégante et bien documentée ; mais ses conclusions font de cet animal une créature marine.

Collini faisait, par ailleurs et fort justement, la distinction entre une zoologie des animaux vivants et une zoologie des animaux trouvés à l'état de fossiles, la zoologie fossile devenant pour le naturaliste philosophe un objet d'étude intéressant, en ce qu'elle nous présente presque toujours des animaux qui nous sont inconnus. Ont-ils été détruits par quelque « révolution du Globe »? Plusieurs des idées de Collini se retrouvent dans le prospectus de Cuvier (1800–1801) rédigé pour lancer son grand ouvrage sur les « ossemens fossiles ». Ces idées n'étaient naturellement pas propres à Collini et elles reflètent clairement l'esprit des Lumières. Cuvier utilisera ces idées pour obtenir le parrainage de l'Institut de France pour son projet d'étude des fossiles de quadrupèdes. Dans son discours préliminaire, Cuvier abordera la manière dont les fossiles sont formés dans les sédiments aquatiques et terrestres, et expliquera pourquoi les vertébrés quadrupèdes terrestres sont préférables aux invertébrés marins pour étudier la vie des fossiles, et pourquoi les espèces fossiles diffèrent des espèces actuelles, autant d'arguments qu'il utilisera après la lecture de Collini.

Collini ne donna pas de nom au spécimen qu'il décrivit et il ne chercha pas à le classer ; il suggéra que cet animal pût être amphibie. Hermann conclut qu'il pouvait être un intermédiaire entre les mammifères et les oiseaux. C'est Cuvier qui reconnaîtra la nature reptilienne de cet animal.

La correspondance entre Cuvier et Soemmerring montre un désaccord sur la nature de cet animal, que Soemmerring avait nommé *Ornithocephalus* [28]. Après 1812, Cuvier complètera sa description grâce à des dessins réalisés en Allemagne en 1812 par Alexandre Brongniart lors de sa visite à Munich en compagnie de Constant Prévost. Il reçut de Oppel une excellente illustration en 1816 ; en 1824, Cuvier pourra utiliser les éléments tirés d'un nouveau spécimen décrit par Soemmerring, ce dernier persistant dans son interprétation avec une reconstitution très proche d'une chauve-souris (Fig. 5).

4. Conclusion

L'envoi par Jean Hermann à Georges Cuvier de la première reconstitution d'un ptérosaure n'a pas changé l'interprétation que ce dernier se faisait de la nature reptilienne du ptérodactyle. Mais la lettre d'Hermann eut le mérite d'attirer l'attention de Cuvier sur le spécimen étrange décrit par Collini et elle fut décisive, en poussant Cuvier à effectuer des recherches ultérieures sur les quadrupèdes fossiles.

Cet épisode de la description du ptérodactyle nous informe aussi sur les pratiques taxonomiques de la fin du XVIII^{e} et du début du XIX^{e} siècle. Il nous montre aussi que Cuvier se refusa à donner une représentation de l'animal dans son ouvrage sur les *Ossemens fossiles*, tandis que la reconstitution proposée par Soemmerring fut reprise par Buckland dans son traité Bridgewater de 1836. C'est donc une image proche de celle des chauves-souris qui fut utilisée durant tout le XIX^{e} siècle et une bonne partie du XX^{e} siècle. Si Cuvier ne publia pas le document d'Hermann, il ne manqua pas de souligner, en écrivant à propos du Ptérodactyle, qu'« on pourrait le dessiner à l'état de vie ; mais la figure que l'on obtiendrait serait des plus extraordinaires, et semblerait, à ceux qui n'auraient pas suivi toute cette discussion, le produit d'une imagination malade plutôt que des forces ordinaires de la nature. »

1. Introduction

Pterosaurs are among the most chimeric creatures known from the fossil record. Since their discovery in the late 1700s, their mode of flight, their stance and gait on the ground, their wings, and their body coverings have all been reconstructed in very different ways [13,21,38]. This is no less true in the present era than it

was two centuries ago, despite great advances in anatomical knowledge based on spectacular specimens and new techniques [33,34].

The first complete pterosaur specimens were found in the famous calcareous marine limestones of the Late Jurassic of Bavaria, in and around Solnhofen and other villages of the Altmuhl Valley [4,8,9,19,20,28]. Fragmentary finds were later reported from Early Jurassic rocks in England [3] and southern Germany [22,31] through the early 1800s, and by the mid-1800s a variety of complete pterosaurs was known throughout the Jurassic from several European countries [38]. By mid-century, Cretaceous pterosaurs were also known from fragmentary remains in England; Seeley catalogued many of them in 1870.

Although pterosaurs were among the strangest creatures yet discovered from the fossil record, there were very few scientific reconstructions or restorations of them until the later 19th century [21]. Detailed drawings of specimens were published by many scholars, including Collini, Cuvier, Soemmerring, Oken, Theodori, Buckland, Meyer, and Owen, but there were very few attempts outside the popular literature to reconstruct the animals in their natural poses, or to restore their soft parts. This may have partly reflected a perceived lack of indisputable facts of anatomy, because there was considerable disagreement about even basic skeletal features. But the reluctance to reconstruct pterosaurs also reflected a profound uncertainty about their 'affinities' (which are not in any sense evolutionary relationships), functional morphology, and ecological habits.

In 1925 the German paleontologist Othenio Abel published a well-known book on the history and methods of reconstructing fossil vertebrates (*Geschichte und Methode der Rekonstruktion vorzeitlicher Wirbeltiere*) [1]. He included many drawings of pterosaurs, ranging from realistic to fantastic. In his view, the oldest surviving restoration was by Johannes Wagler [36], who had restored the pterosaur as a swimming animal. However, there was actually an older restoration [21] by Samuel Theodor von Soemmerring [29] that had a double influence (see below): first, it was widely copied and reprinted by other paleontologists; and second, it visualized the pterosaur with a bat-like form [21], because Soemmerring thought the animal was a prehistoric bat. Despite Cuvier's protestations that the animal was clearly a reptile, and in no way bat-like or mammal-like, this image survived to become the dominant icon of pterosaur representations until the late 1980s [21].

Like others who have reviewed the history of pterosaur restorations, Abel knew that there was yet an older drawing, even though neither he nor any other paleontologist of his time had seen it. He knew because Baron Georges Cuvier had written about it in 1809 in the *Annales* of what was then called the 'Musée d'histoire naturelle', and in his *Ossemens Fossiles* of 1812 and later editions. Cuvier had received the drawing from Professor Jean Hermann of Strasbourg. But Cuvier never published this restoration, and it appeared to be lost. Following convention, we denote *reconstructions* as illustrations that reassemble the skeletal parts, usually with the indication of missing elements, in more or less natural posture; *restorations* are attempts to add the soft tissues of the body, and often to portray the animal in its natural habitat, performing characteristic behaviors. The earliest illustration of a pterosaur specimen was by Collini [4]; the earliest reconstruction of a pterosaur was by Soemmerring [28, see 37,38]; the earliest published restoration was by Soemmerring [29] (see [21]); and the earliest known restoration, though unpublished, was by Hermann, which we illustrate here.

The purpose of this paper is to report on what eventually happened to Hermann's restoration, which turns out to be more unusual than either Abel or anyone else seems to have imagined. We situate this sketch, and several other unpublished drawings that were made for Cuvier, within the early history of the understanding of pterosaurs, and to explain some of the classificatory questions at stake – which had rather different imports than they do today. Finally, we show how Hermann's letter led Cuvier to a close examination of Collini's [4] original paper on the animal – a paper that he used not only to satisfy himself about the osteological anatomy of the new creature, but to adapt many theoretical and rhetorical devices for his rapidly evolving prospectus on his projected *magnum opus* on fossil quadrupeds.

2. Hermann's unusual restoration

In March 1800, Georges Cuvier received a letter from his friend, Professor Jean Hermann of Stras-

bourg, near the German border of France. These were turbulent times, as Hermann's letter reflects; only four months before this letter was written, Napoleon had succeeded in abolishing the Directory in Paris, the council of Five Hundred that had become the main governing body after the Revolution, and having himself established as Consul. He had also just carried out a highly successful military campaign in Egypt, which also succeeded in bringing back tremendous collections of both antiquities and biological specimens to Paris [15]. And he was about to invade the western provinces of Germany. On 25 April 1800, General Moreau crossed the Rhine with the French armies and invaded successively the 'Schwäbische' basin and the Bavarian plateau before entering Munich in July. Alongside the Army were 'Commissaires du gouvernement français en Allemagne' for Sciences and Arts, whose task was to select and to bring to Paris books, paintings, sculptures and scientific objects, called 'saisies et offrandes volontaires' (!). This was done by François-Marie Neveu in Munich from July to December 1800 and by Jean-Baptiste Maugérard from 1802 to 1804 in the Rhine departments on the left side of the river (including the city of Mayence). The French commissioners were sometimes helped by German collaborators like Anton Keil, but, in this case, the German scientist Baron von Moll successfully used his friendship with René-Just Haüy, the mineralogist of the Museum in Paris, to obtain protection from the French army and to avoid the exile of the Bavarian Earth Sciences collections. The story of this confiscation is well described in an excellent book just published and entitled *Patrimoine annexé* [25].

Although far from the French capital, Strasbourg did not escape the political and social turbulence of those years. Hermann's brother, Jean Frédéric, a professor of law at Strasbourg and later its mayor, actively protested government policies and was particularly opposed to the suppression of the University of Strasbourg in 1799 [32]. Yet despite regime changes and seesawing politics, the normal business of scholarship persisted. Jean Hermann, like most savants of the time, worked on a variety of subjects, but was mainly a professor of medicine and a well-recognized naturalist [35]. He wrote to Cuvier in this instance to advise him of a most unusual fossil that Hermann himself does not appear to have seen, and of which Cuvier had apparently never heard. However, Hermann had reason to think that it might be coming Cuvier's way.

Cuvier had only been in Paris for five years, but he was already well known nationally and internationally. In November 1806, he wrote to G.L. Duvernoy that problems with his eyesight made it no longer possible for him to dissect marine invertebrates under the microscope, and that henceforth he would limit his attention to fossil bones brought to him from Montmartre. Before 1800 Cuvier's papers are rather evenly divided between vertebrates and invertebrates; after 1803 there are very few invertebrate papers [27]. By 1798 he had decided to publish a full compendium of what was known of fossil vertebrate remains, for reasons discussed below. He made plain his intention to establish a network of communication of scientific knowledge in natural history, particularly vertebrate zoology and paleontology [5,6,7,24], including the exchange of papers, illustrations, and casts of specimens. He was in constant communication with scholars all over Europe, from Buckland to Goethe; he had grown up in southwestern Germany, and had many ties to the region. So it is not at all strange to find Hermann writing to Cuvier (13 Vendémiaire, an 8 [= 4 March 1800]; MS 629V: 147. MS numbers refer to the archives of the 'Bibliothèque centrale' of the MNHN, Paris):

> *Mon frère vous remettra, mon cher, une feuille avec deux esquisses d'un animal. Ignorant si vous vous êtes proposé de parler de tous les animaux fossiles sur lesquels il est possible de dire quelque chose d'assez déterminé, ou seulement sur ceux que vous pouvez examiner vous-même, je vous rends très attentif à tout événement au squelète très singulier décrit et représenté par Mr. Colini dans le Vième volume des Mémoires de l'Académie de Manheim, partie physique. Si ceux qui ont été chargés de piller vandalo-républicainement le cabinet de Manheim – sur lequel acte j'ai lu une lettre d'un savant distingué qui s'en est plaint amèrement – s'y sont bien connus, ils auront enlevé sans doute la pièce et elle sera déjà en votre possession. Pour la belle et unique tête de méduse sur un schiste de Boll, je pense qu'ils ne l'auront pas manquée.*
>
> *Je voulais depuis longtems publier un mémoire sur cette pièce et montrer que l'animal doit avoir formé une espèce plus intermédiare entre les mammifères et les oiseaux, mais la figure qu'il eût fallu faire graver y a toujours mis un empêchement.*

Aujourd'hui que notre paternal gouvernement me dégoûte de plus en plus de toute entreprise, j'en abandonne le projet. Je vous en communique mes premières idées; voyez ce que vous voulez en faire, vous êtes juge bien plus compétent que moi. Je serais flatté si vous ne trouviez pas tout à fait inadmissible mon idée.
J'ai l'honneur de vous saluer,
Hermann.

Our translation follows. Note that Hermann specifies that the new animal must have formed a more intermediate species *between mammals and birds* than bats do.

"My brother [Jean Frédéric] will bring you, dear friend, a folder with two sketches of an animal. Not knowing whether you plan to discuss every fossil animal about which it is possible to say something that is fairly definite, or whether you only want to consider those that you have been able to examine yourself, I draw your keen attention in any event to the very singular skeleton described and illustrated by Mr Collini in the 5th volume of the *Mémoires* of the Academy of Mannheim, physical part. If those who have been assigned the vandalo-republican pillaging of the Mannheim collection – on which act I have read a letter from a distinguished colleague who complained bitterly about it – are aware of this specimen, they will have no doubt taken it and it will already be in your possession. I expect that they will not have missed the beautiful and unique medusa's head in the schist from Boll.
"I have wanted for a long time to publish a memoir on this piece and to show that the animal must have formed a more intermediate species [i.e., than bats] between mammals and birds, but the figure that needs to be engraved has always been an obstacle. The way things are going now, as our paternal government disgusts me more and more with every enterprise, I'm abandoning the project. I'm sending you my preliminary ideas about it; see what you'd like to do with it, you're a much more competent judge than I am. I would be flattered if you didn't find my idea completely inadmissible.
I have the honor of greeting you,
Hermann."

This letter is revealing for a number of reasons. The 'very singular skeleton' to which Hermann refers was none other than the first pterosaur to be described, and the one on which the term *ptéro-dactyle* – Cuvier's [8] name for what the Germans eventually called pterosaurs – would be based. Actually, in the title of Cuvier's 1809 paper, the first in which he named the animal, it is spelled *petro-dactyle*, which would more literally mean 'rock-finger' rather than 'wing-finger'. Cuvier corrected this when he essentially reprinted this article (like most other original entries) in his first edition of *Ossemens Fossiles* [9]. He did not latinize the name and did not provide a specific epithet. His 1809 paper only went as far as the title: *Memoir on the fossil skeleton of a flying reptile from the Eichstätt area, which some naturalists have taken for a bird, and for which we create a genus of Saurian, under the name of Petro-Dactyle. Ornithocephalus antiquus* Soemmerring 1812 was the first latinized binomial epithet for a pterosaur. Oken [19 (p. 246)] first latinized the name *Pterodactylus*, based on Cuvier's title of 1809; he regarded it as a better name than *Ornithocephalus* ('bird-head') because the long wing-finger was so distinctive. At the time, it was the only specimen known, and it had not even been named. It had been first described in 1784 by Alessandro Cosimo Collini, a Florentine who had been secretary to Voltaire for some years and eventually took over the natural history cabinets in Mannheim. Peter Wellnhofer [37,38] has written succinctly and with great accuracy about Collini, Cuvier, Soemmerring, and the early discoveries and ideas about pterosaurs (see also Müller [17] and Wenzel [39]). Although of necessity we cover some of the same historical ground here, we can scarcely improve upon the excellent accounts in his works.

Hermann's letter brought Cuvier the first notice of this animal, greatly piqued Cuvier's interest, and directly stimulated two decades of Cuvier's intermittent writings on pterosaurs. Cuvier clearly had not known of the specimen, but must have immediately looked up Collini's paper. This is evident because he mentioned the animal, which he realized was a flying reptile, a few months later in his prospectus of what would become a great series of papers culminating in *Ossemens Fossiles*. Its publication date is usually given as 1801, but it was actually first published in December 1800 by Baudouin, the official publisher of the Institut de France [27]. (It was published in 1801, with corrections, in the *Journal de Physique, etc*., also an official Institut publication, and in the *Magasin Encyclopédique* for

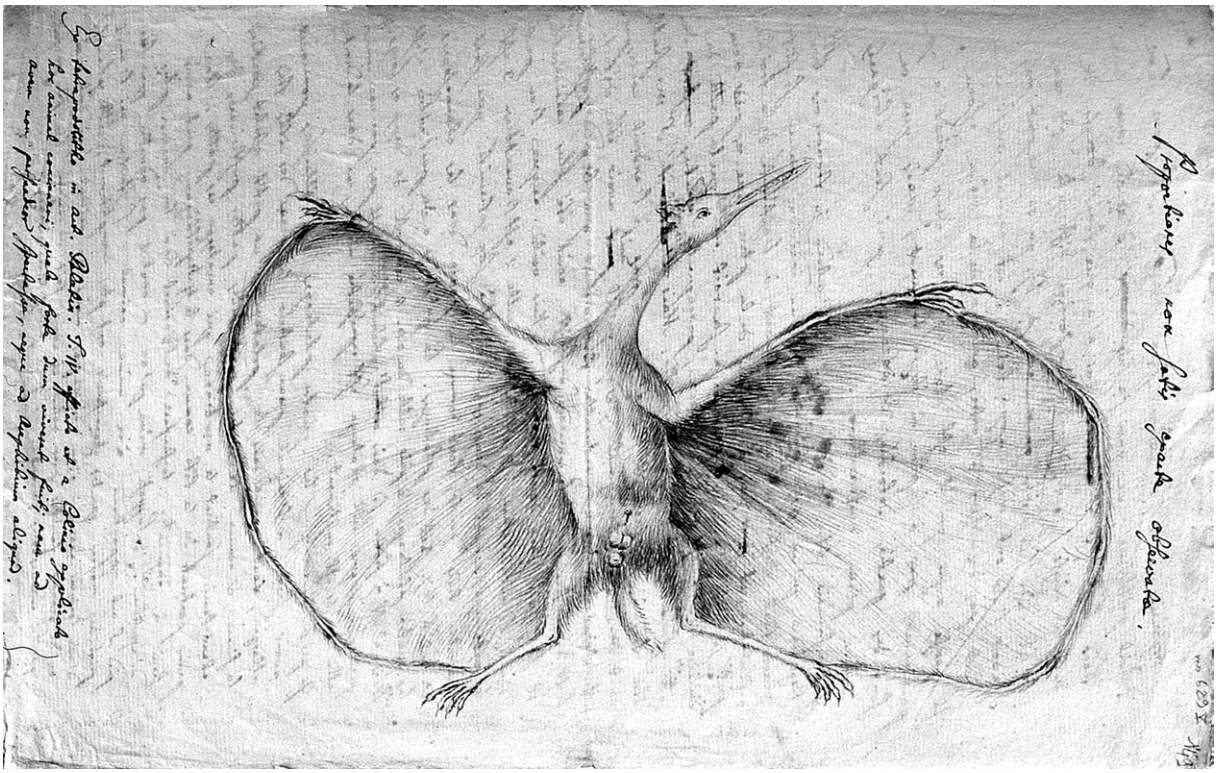

Fig. 1. First of two sketches by Professor Jean Hermann of Strasbourg, sent to Cuvier in 1800, of the mysterious animal described by Collini (1784). Hermann seems to have been the first to recognize the animal as winged (Ms 629V. f° 149). Photo: Bibliothèque centrale MNHN, Paris, France.

Fig. 1. Le premier des deux schémas réalisés par le professeur Jean Hermann, de Strasbourg, envoyé à Cuvier en 1800, représentant le mystérieux animal décrit par Collini en 1784. Hermann semble avoir été le premier à reconnaître la nature ailée de l'animal (Ms 629V. f° 149). Photo : Bibliothèque centrale MNHN, Paris.

1801 [7e année 1: 60–62].) The Institut authorized Cuvier's undertaking on 15 November 1800, and Cuvier dated his prospectus 1 December 1800. So these events followed each other closely.

Hermann feared that the specimen might already be pillaged and removed from Mannheim. As it turned out, it had not been taken and sent to Paris by Napoleon's invading armies (as, for example, the mosasaur was formerly brought from Maastricht by General Pichegru's army); instead, the entire natural history cabinet at Mannheim was removed to Munich at least by 1802, after the death of the last member of the Bavarian lineage in Mannheim and the inheritance by his successors in Munich [37,38,p.23]. Hermann does not seem to have been aware of this, nor to have seen the actual specimen himself (Mannheim is 130 km from Strasbourg). Instead, Hermann examined Collini's paper, and sent Cuvier two pages of notes on Collini's description and interpretation of the animal (MS 629V: 147–150). Unfortunately, Hermann could do no more for Cuvier; he died on 4 October 1800.

Of particular interest are Hermann's two sketches (Figs. 1 and 2), reproduced here for the first time, which restore the animal *revêtu de son poil* (restored with its hairy covering), as Cuvier [8,9] noted in acknowledging Hermann's idea. Several features are immediately striking. As with most pterosaur specimens known even today, there was no evidence for a hairy covering, or even for a wing membrane. However, Hermann (like Cuvier) recognized that it must have had wings, and that this must have been a flying animal. And, because Hermann thought it was an intermediate between quadrupeds (essentially, mammals) and birds, he thought it justified to restore it with fur, external pinnae of the ears, a brushy tail, and mammalian genitals. He also suggested a membrane of skin

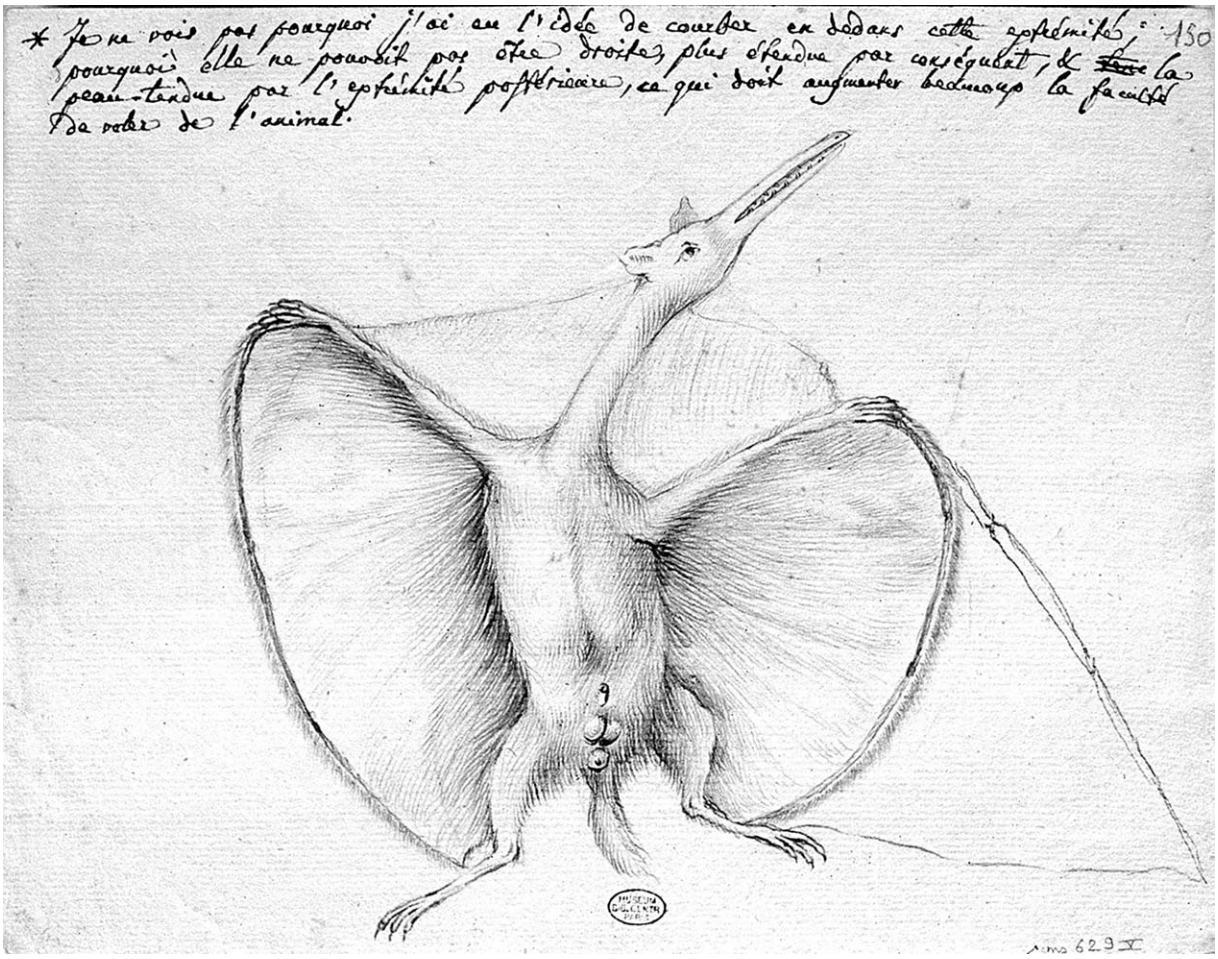

Fig. 2. The second sketch sent by Hermann to Cuvier in 1800. These are the earliest known restorations of a pterosaur, although they have never been published until now (Ms 629V, f° 150). Photo: Bibliothèque centrale MNHN, Paris, France.
Fig. 2. Le second schéma adressé par Hermann à Cuvier en 1800. Ces schémas constituent les premières reconstitutions connues d'un ptérosaure, bien qu'ils n'aient jamais été publiés jusqu'à présent (Ms 629V, f° 150). Photo : Bibliothèque centrale MNHN, Paris.

from the base of the skull along the neck and arm out to the wrist, much as in dermopterans and some bats. One of the sketches portrays this, though it may have been added after the rest of the drawing.

Hermann's reconstruction of the wing is notable: he made the bones of the wing finger curve unnaturally so that the wing tips reach the feet. In what appears to be a later addition, the right side of the drawing shows straightened wing phalanges and an extended trailing edge of the wing membrane. A note appended by Hermann to the top of the second sketch explains: "I don't know why I had the idea of curving this extremity back toward the inside; why couldn't it have been straight, and therefore more extended, and the skin supported by the posterior extremity, which would have greatly improved the animal's ability to fly [?]"

Hermann also included with his letter a brief description of the specimen, in which he pointed out many details in which he disagreed with Collini's [4] original account, and found strong similarities to both birds and mammals. He concluded that the animal was an excellent flyer, and "would have made a much better link than bats between mammals [quadrupeds] and birds." Hermann uses both "mammals" and "quadrupeds" in his letter to Cuvier, but he specifically means mammals; the terms were often used interchangeably. For example, Cuvier's 1798 prospectus for what became *Ossemens Fossiles des Quadrupèdes* contains

only discussions of mammals, though his eventual work included reptiles as well [9–11].

3. Cuvier's attempts to study the *ptéro-dactyle*

Cuvier tried to get access to the specimen, which he immediately realized was not a marine animal as Collini had thought, nor a mammal as Hermann thought, but a reptile. When he found out that the collection had been transferred to Munich, Cuvier asked the baron of Moll, whom he [8,9] described as a "celebrated mineralogist", if he could see it, but the baron could find no trace of the specimen; and so Cuvier was forced to rely on Collini's [4] description, which he realized was problematic in many respects. But the specimen could not be found because it was being studied by Samuel Thomas von Soemmerring, one of the most respected German natural historians of the late 18th and early 19th centuries [16 (p. 95)], who had become curator of the collection in Munich.

Soemmerring and Cuvier knew each other, of course, and regarded each other with great collegial respect; so it is not clear why Cuvier did not apply directly to him. Eventually Soemmerring was apprised of Cuvier's request, but, ironically, it was just after Soemmerring had submitted his manuscript on the specimen to press. He wrote to Cuvier (16 January 1811, MS 629V: 139) of his distress at not having seen Cuvier's 1809 paper (it had evidently not yet been received by the library at the Academy in Munich), and of his intent to please Cuvier by a description of this animal to include in Cuvier's projected compendium of fossil quadrupeds. He was further distressed that Cuvier had to rely on Collini's drawing, which persuaded Cuvier that the '*incognitum*' was a reptile (and not a mammal as Soemmerring concluded). Soemmerring noted with deferential regrets that he had added a postscript (*Nachtrag*) to his paper in press, because he could not retract it for revision, to address Cuvier's conclusions.

Cuvier shot back a response the day after receiving Soemmerring's letter (its draft is MS 629V: 136–138), and he was not pleased. He complained that if he had had to rely on Collini's erroneous figure, it was because no one in Munich could find the original specimen, even though Soemmerring had assured him that it had been preserved during the move like a precious relic. He reproached his German colleagues for their lack of communication and responsiveness, inasmuch as they had all been given free access to the Paris museum specimens, yet had not responded to his requests for illustrations of the Munich ones that he needed. It was clearly frustrating to Cuvier that he did not have up-to-date information for his *Ossemens Fossiles* [9]. He continued to solicit drawings and observations of the specimen from other colleagues. And he eventually obtained a cast of the specimen from Soemmerring in 1818. The cast, which is adequate for general features but not sharp on many critical details, is still in the Museum, and a letter of transmission from Soemmerring that accompanied it is in the archives of the 'Bibliothèque centrale' of the Museum (MS 629 V: f°140). But Cuvier and Soemmerring continued to disagree about the animal for many years, and many of the arguments in their letters are repeated in their published works.

4. The 'affinities' of the pterodactyl: evidence and arguments

Accounts of the early discoveries and understanding of pterosaurs frequently focus on attempts to classify the animal. This approach is useful because classification reflects the use of critical features to place a new form among others most like it, regardless of the systematic philosophy or the objective of the classification. However, in the late 18th century, classification did not reflect phylogeny; similarities were used to arrange organisms with each other, but did not necessarily imply genealogical relationship. These 'affinities', a term that persisted until at least the 1870s (e.g., Seeley [26]), were mainly reflections of plans of organization that used key characters to establish a 'natural system' of living things (e.g., Stevens [30], Padian [21]).

We could, of course, simply allow Cuvier to enter the scene after decades of uncertainty and unhesitatingly pronounce the pterosaur a true reptile – which he did – but this would oversimplify the situation. The early discussions about the *ptéro-dactyle* were intimately connected to questions not only of taxonomy but, more importantly, of what fossil remains were and what they signified. Cuvier was not alone in realizing what was at stake.

It turns out that the very first description of a pterosaur, by Collini in 1784, was instrumental to the history of these questions, in a way not heretofore recognized. Collini had been in charge of the royal natural history cabinets in Mannheim for twenty years, and Cuvier [8,9] highly praised his curatorial abilities. He described Collini as having had "wit and wisdom, but little in the way of real knowledge of natural history and anatomy," a view that Soemmerring [28] independently voiced. But even though he may not have been primarily an anatomist, Collini was a highly educated and perceptive man who wrote succinctly and elegantly about this new animal and many other finds, separating observation and inference, and advancing opinions judiciously.

Most historical treatments of Collini's paper have focused on his reasoning that the animal was neither a bird nor a bat, and his speculation whether it could be some kind of amphibian (the term did not have the taxonomic meaning that it does today; it merely denoted an animal that can live on land and in the water). Collini concluded that we must look for its "original" among the marine animals, but this too is not a simple statement. Cuvier repeated verbatim Collini's description of the specimen's particulars, and then added three pages of his own comments and corrections. But he did not discuss Collini's account of how this animal (and other fossils) should be understood in the first place. This is revealing, because in his 1800 [7] prospectus for *Ossemens Fossiles*, he directly addressed and sometimes even reiterated many of Collini's (1784) philosophical considerations about fossil animals.

5. What Cuvier got from Collini

To introduce his paper, Collini noted that there is an effect a "double Zoology," one based on living animals and one on those that are found as fossils. The fossil ones are not the same as the living ones, but it is not clear why. We know nothing of their "originals" – that is, the living animals that left these fossil remains. If they live today, terrestrial forms could persist in unexplored lands, and marine forms in the depths of the oceans. But what if they had been destroyed by some "revolution of the Globe"? What effect would this have on what are often called the "ladders of life" or "scales of beings" [*échelles des Êtres*], which assume no possibility of a missing part? Should we assume that this would be a serious problem, given that a man can lose a digit or a hand and still remain a man? There are various theories of the Earth, he concludes, and this is not the place to discuss how well they variously correspond to known facts. But is it not of some interest that in the animal kingdom (and he also thinks this for the plants), the fossil forms are so completely different from the living ones?

> *La zoologie fossile, qui pourrait paraître une occupation inutile ou minutieuse, devient pour le Naturaliste philosophe un objet intéressant, en ce qu'elle nous présente presque toujours des animaux qui nous sont inconnus. Le grand tableau de la Nature se perfectionne par ce moyen, puisque de nouveaux êtres viennent y occuper une place dans les espaces que nos imperfections et les bornes de notre entendement ne nous permettront jamais de remplir. Si au nombre des animaux vivans qu'on est jusqu'à présent parvenu à connaitre, on joint ceux qu'on trouve quelquefois enfermés dans les entrailles de la terre et que nous ne connaissons pas, il en resulte une double Zoologie, l'une vivante, l'autre morte, ou fossile. Je dirais presque que l'on connaît tout aussi imparfaitement l'une que l'autre.*
>
> *Les animaux dont on trouve, dans l'intérieur de la terre, ou l'empreinte sur des pierres, ou quelques restes osseux isolés, ont été ou terrestres ou aquatiques. S'ils ont été aquatiques, par quelle vicissitude ont-ils été portés dans le sein des montagnes? S'ils ont été terrestres, et d'une espèce qui approche d'une des espèces connues, par quelle vicissitude encore leurs cadavres se trouvent-ils enterrés dans des pays dont le climat est si différent de celui dans lequel vivent de nos jours les originaux de ces animaux? Pourquoi, par exemple, trouve-t-on en abondance, dans des pays très froids, des ossemens fossiles d'animaux qui ne peuvent vivre que dans des pays d'un climat fort chaud? Si les animaux, soit aquatiques, soit terrestres, auxquels ont appartenu ces fragmens, ces restes d'ossemens, ces squelettes et ces carcasses fossiles, nous sont inconnus, que sont devenus leurs originaux? Existent-il encore ces originaux dans les profondeurs des mers qu'ils ne quittent jamais pour se montrer à nos yeux, ou habitent-ils*

des contrées et des parages dans lesquels les hommes n'ont pas encore pu pénétrer? Dans l'un et dans l'autre cas, n'est-ce pas un avantage de parvenir à connaître, par ces restes fossiles, des animaux que nous ne pourrons peut-être jamais connaître d'une autre manière? Si ces originaux n'existent plus, par quelle révolution du globe l'espèce s'en est-elle détruite? Quelles sont les circonstances qui y ont donné lieu?
[...] il y a une quantité de productions fossiles, connues en général des Naturalistes sous le nom de Pétrifications dont on ne trouve point les originaux. Les coquilles fossiles sont dans ce cas. La plupart d'entr'elles sont des espèces ou des variétés qui nous sont inconnues. Cette observation a lieu encore pour les Polypiers fossiles ; elle a lieu pour les Poissons pétrifiés, puisqu'il y en a peu qu'on connaisse, et peu dont on puisse dire avec certitude, voici son original. On peut dire la même chose des végétaux fossiles. Qu'on compare les bois pétrifiés aux bois naturels auxquels ils paraîssent ressembler ; on n'en pourra pas produire deux échantillons, l'un naturel l'autre fossile, dont on puisse être fondé à dire, que l'un est le vrai original de l'autre. Ces espèces de fougères et d'autres plantes fossiles dont on trouve les empreintes sur des substances pierreuses, diffèrent toujours des plantes qu'on connait. N'est-ce donc pas un phénomène particulier que le Règne animal fossile soit presqu'entièrement différent du Règne animal actuellement existant, c'est-à-dire, différent des animaux qui sont jusqu'à présent parvenus à notre connaissance? L'un et l'autre de ces Règnes contribuent à nous donner une connaissance plus étendue des productions animales, et une idée plus auguste de la variété des Êtres.

Many of these ideas show up in the introduction to Cuvier's [6,7] prospectus for his *Ossemens Fossiles* – and they were *not* present in his 1798 versions. Cuvier [6,7], for example, speaks of 'revolutions of the globe', and how they brought the world to its present state. He acknowledges frankly that fossil mammals are not of the same species as any living mammals. He notes that fossil animals from the aquatic realm are now found in rocks on land, where they clearly did not live. He addresses the problem that many fossil animals are found in lands with climates that clearly would have been inhospitable to them in life. Finally, he states that we must understand these animals through analyzing their anatomy, discerning their functions, and reconstructing their ways of life.

Not all of these ideas were original to Collini, of course, and we do not wish to overstate his influence on Cuvier's ideas expressed in 1800; but Collini's arguments, as well as his rhetorical approach, were highly individual and clearly reflect the spirit of the Enlightenment (to which he no doubt owed something to Voltaire). Cuvier repeated many of his ideas to advantage in his prospectus, but with a twist. His purpose was to obtain from the Institut de France the authority and support for a long-term study of fossil quadrupeds. He acknowledged the wealth of fossil remains of all kinds of organisms, but said that in order to understand the life of the past, the revolutions of the Globe, and the circumstances that caused them (again echoing Collini's words), the most appropriate subject of study are fossil quadrupeds. This is because we probably do not have a very complete knowledge of aquatic forms (many of which may be inaccessible to us in the ocean depths), but our knowledge of quadrupeds, especially mammals, is fairly complete. Maybe we have overlooked some small forms in distant lands, but these are relatively insignificant; we certainly know nearly all mammals of substantial size.

Cuvier repeated these same ideas in the 'Preliminary Discourse' to the first edition of his *Ossemens Fossiles* [9]. They constituted some of his primary theoretical arguments [24] (text 19, sections 26, 27, 28, 32, 33): on how fossils are formed in terrestrial and aquatic sediments (26), on why terrestrial quadrupeds are better than marine invertebrates for studying fossil life (27), on why nearly all living terrestrial quadrupeds must already have been discovered (28), and on why fossil species are different from living species (32, 33). All these concepts first found voice in Cuvier's [6] perspective, after he read Collini.

So it was that Collini's arguments, which Cuvier had carefully read in the very months before he published his prospectus, became much of the rhetorical foundation of the rationale of Cuvier's monumental work on fossil quadrupeds.

But what was Collini saying about the affinities of the new animal? The fact is that he did not commit himself; he did not give it a name, and did not classify it at all. He recognized how problematic it was. When

he suggested that it might be amphibious (*Amphibie*) he was not relating it to a salamander, but saying that it might be an animal capable of living in both terrestrial and aquatic realms; the Class Amphibia would not be named for most of a century afterward. Crocodiles, because they lived in both realms, could be considered *Amphibie*. Soemmerring [28] attributed just such an assignment (*Amphibium*) to Cuvier because he regarded the new animal as a reptile; but Soemmerring also said that Collini considered it a fish, which is equally inaccurate. Similarly, when Collini surmised that its "originals" might be found among marine animals, he did so because he had dismissed birds and bats for various reasons; he did not seriously consider that the animal might be a reptile. As noted above, there were likely to be more unknown things in the sea than on the land, so it was logical to suspect that this was a marine animal, simply because it was so unusual (and was found in association with marine animals). In support, Collini mentioned the long beak and the shape and number of the teeth, but this does not seem to have impressed later workers. Collini could not imagine to what use the forelimbs would have been put. In the end, he concluded, one would have to know more about the ways of life of the animal, its habits and environments, before being able to say more.

Collini's description of the anatomy of the animal was correct and ingenious in many respects, but he misidentified a number of bones and other structures. The anatomists who followed him did not hesitate to point this out, but they did not always agree on what they saw. Hermann, in his 1800 letter to Cuvier, was apparently the first to recognize that the elongated finger would have supported a wing, though it is doubtful that anyone except Cuvier knew this, because Hermann did not publish his observations. Hermann clearly stated several times that the animal would have flown like bats do. He allowed that the interior of the skull and the lower jaw showed the characteristics of birds; but the ribs lacked uncinate processes and there was no sternum or wishbone, and the pelvis, tail, and metacarpal digits forced him to reject this idea. Hermann correctly identified the bones of the forelimb, and rejected Collini's idea that this could be a marine animal because marine animals have foreshortened limbs, not elongated ones; note that his reasoning is not related to taxonomy, but to functional ecology. "Everything indicates an animal with mammaries", he stated, but provided no features or arguments in support of this. Again, apparently more for ecological reasons than for structural ones, Hermann concluded that the animal "should have made a better link than bats between quadrupeds [by which, as he says in his letter, he means mammals] and birds." Most authors have (of necessity) repeated Cuvier's misstatement that Hermann took the new animal for an intermediate between birds and bats.

In his 1800–1801 prospectus for *Ossemens Fossiles*, Cuvier said of the animal only that it was a reptile: "it was small, and seems to have enjoyed the faculty of flight, as the small lizard called the dragon [*Draco*] does today." *Draco*, of course, glides and does not flap, and uses its ribs, not its forelimbs, to support its airfoil. Cuvier obviously knew this, and in his 1809 work (and later) he stated that the animal was a powerful flyer, at least as much so as bats. But he wanted to emphasize that it was a reptile; in fact, he noted (1824, Vol. V, Part II, p. 378) that as soon as he saw the form of the pubis, he wrote to Hermann that it was a reptile, and he wrote to Soemmerring in 1811 that the cylindrical form of the quadrate alone told him this, as did the homodont teeth and the phalangeal formulae. Wellnhofer [37 (p. 537)] noted that E. Buffetaut drew his attention to a mention of the specimen by F.M. Daudin in an 1803 edition of his *Histoire naturelle, générale et particulière des Reptiles* (vol. 8, pp. 276–296) [12]. Daudin calls the animal "a saurian related to the dragons" [*Draco*] (*un saurien voisin des dragons*), but provides little additional information or reasoning. Inasmuch as Cuvier had alluded to *Draco*, though not as a relative, in his 1801 prospectus, it seems likely that Daudin had seen Cuvier's statement and was offering a somewhat altered version of it. Here is a marked shift in reasoning about affinities: instead of using general functional or ecological analogies, or of simply rejecting affinities on the basis of differences from known forms, Cuvier was singling out specific features that allied the unknown animal with known forms. Even when he rejected Blumenbach's [2] suggestion that the animal was a shorebird (*palmipède*), he did so by specifying key avian features that the *ptéro-dactyle* lacks (larger ribs, uncinate processes, a single metatarsal bone, a wing with only three joints after the forearm; etc.) and pointing out its reptilian features.

6. The dispute between Cuvier and Soemmerring

The correspondence between Cuvier and Soemmerring, and their respective publications in this regard, likewise reflect not the use of a general *Gestalt*, but a conscientious sifting of characters that affirm or reject the affinities of the *ptéro-dactyle*. Cuvier and Soemmerring continued to disagree about the details and affinities of the specimen, although in their first correspondence (in 1811) Cuvier rhetorically acceded to most of Soemmerring's interpretations, (perhaps only) because Cuvier had not seen it. But he held firm on some points. The homodont conical teeth were not at all mammalian, he said; Soemmerring had incorrectly followed Geoffroy Saint-Hilaire's work on mammalian teeth, which did not take into account developmental differences (Geoffroy, Cuvier said, is not an anatomist). Having just completely surveyed teeth for his great work on comparative anatomy, Cuvier informed his colleague of the law that *the back molars never vary in number or shape in any natural genus*. He also criticized Soemmerring's reliance on skull and jaw proportions in bats to establish affinity. And he insisted that the phalangeal formula was not like that of any mammal.

In his publications (e.g., [9,10]), after listing the specific features that made the *ptéro-dactyle* a reptile (quadrate, pubis, homodont teeth, phalangeal formulae, etc.), Cuvier stated with great satisfaction that the laws of anatomy have held true even in this so highly modified animal. This point was critical to Cuvier, because he wanted to establish biology as *law-like*, much as Laplace, Lavoisier and others had done for physics and chemistry, the mechanical sciences [24]. Although Cuvier is generally considered a functionalist in the ancient dialectic between form and function, his functionalism was expressed mainly in explaining the correlation of parts and in adaptations to ways of life. Here, he is using diagnostic features of common body plans, as well as knowledge of ontogenetic transformation and generalizations about form and proportion, to undermine Soemmerring's arguments.

Soemmerring [28], for his part, vigorously defended the proposition that *Ornithocephalus* was a mammal, and in fact some kind of primitive bat. There is much in a name here. Cuvier called the animal *ptéro-dactyle* because he realized that the elongated finger supported a wing. Soemmerring named it *Ornithocephalus* in spite of being convinced it was a bat, because it could be distinguished from other bats by its birdlike head. He had dismissed Collini's conclusion that the animal could not be a mammal because its head and beak were too long, pointing to the long skull of *Hystrix*, and noting that once fleshed out the skull would not have looked so much like a bird's. (One has only to look at Hermann's sketch for support, although it is not proportionally accurate; but an image need only recall the familiar in order to be accepted by the mind's eye: [21].) Soemmerring argued that the toothed beak, the long neck, the tail, the clawed hind foot, and the wing bones are more like those of bats, as is the construction of the breastbone and the breadth of the sternum. He admitted that some birds have long necks, but with many more vertebrae; camels and giraffes, among mammals, have long necks with fewer vertebrae, like the *Ornithocephalus*. (Cuvier [1824] correctly responded that the number of vertebrae in different regions of the column corresponded to reptiles and not to mammals.) Soemmerring, having read the single sentence of description in Cuvier's (1801) prospectus, listed 13 differences between *Ornithocephalus* and *Draco*, showing again the reliance on specific features, not ecological similarity, to establish affinity. (Cuvier responded in his 1811 letter that Soemmerring's discussion of this was unnecessary, because Cuvier had not said that the ptéro-dactyle was allied to *Draco*, only that it could fly.) In all respects, Soemmerring found similarities to bats, even though he realized that *Ornithocephalus* differed from living bats; he regarded these features as simply what one might expect in a fossil animal. So, in a completely non-evolutionary context, we find Cuvier on one hand, arguing for diagnostic features to establish the affinity to reptiles, and Soemmerring on the other, relying on different diagnostic features, and on suppositions about apparently primitive features that mask the affinity to bats.

After 1812, Cuvier came to understand the specimen even better. He now had both the illustration and the reconstruction of Soemmerring [28]. Not contenting himself with these versions, Cuvier asked his colleagues Alexandre Brongniart and Constant Prévost, who were passing through Munich in 1812, Wellnhofer [37] gives this date as 1818, but at that time Prévost was establishing a spinning mill with Philippe de Girard near Vienna [14], where he remained from 1816 to

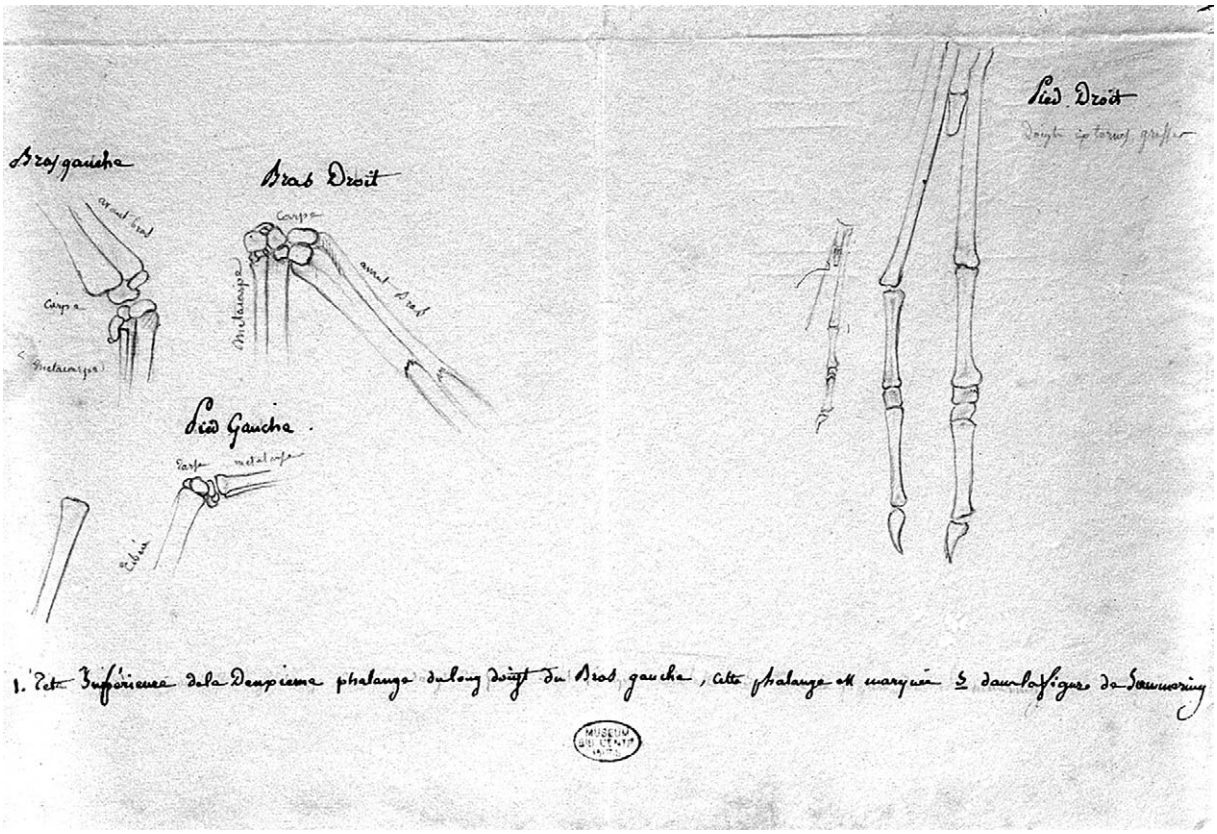

Fig. 3. Drawings of the pterodactyl made for Cuvier by A. Brongniart in Germany. Photo: Bibliothèque centrale MNHN, Paris, France.
Fig. 3. Dessin du ptérodactyle réalisé pour Cuvier par A. Brongniart en Allemagne. Photo : Bibliothèque centrale MNHN, Paris.

1819 without any known research activity. He and Brongniart did their tour of Germany and adjacent regions in 1812 [14: 8–9]. to make him additional drawings, particularly of the wrist, ankle, and digits (Fig. 3), on which Cuvier based other figures in his Plate XXIII (1824). Michel Oppel, an artist and natural historian from Munich, rendered the animal in ink and watercolor at Cuvier's request, and sent the illustration to him in 1816; Cuvier relied on it for his second (1824) edition of *Ossemens Fossiles* (Volume V, Part II, *Sauriens*, Pl. XXIII). Oppel noted in an accompanying letter (MS 629 V: 133–135, including Oppel's painting: Fig. 4) some particular details of the vertebrae and teeth that Cuvier had requested, and added that his drawing differs in some critical respects from Collini's, not just in the bones that Collini omitted, such as the quadrate, but in those that he did not fully illustrate. Cuvier also benefited from Oken's [19,20] description of the noted fossil. Oken agreed emphatically with Cuvier that the animal was a reptile; he said [20 (p. 1795)] that it 'lies between chameleons and crocodiles', and that it was only Collini's incorrect illustration that misled Cuvier in some details.

By 1824, Cuvier was able to add the testimony of a second example of *ptéro-dactyle* to his catalogue. Soemmerring [29] had described a second tiny specimen, also from the Solnhofen limestones, as a new species (*Ornithocephalus brevirostris*), largely on the basis of its very short snout, and provided the first published reconstruction of a pterosaur – in a very bat-like pose (Fig. 5). Soemmerring had written to Cuvier of the new find with some excitement (16 March 1816; MS 629 V: 131–132). To Soemmerring, it showed that (1) in the prehistoric past there were bats that had only four toes and four fingers, in contrast to all known vespertilionids of the present day, which have five; (2) that only one of these four fingers was elongated to form a wing support; and (3) that the

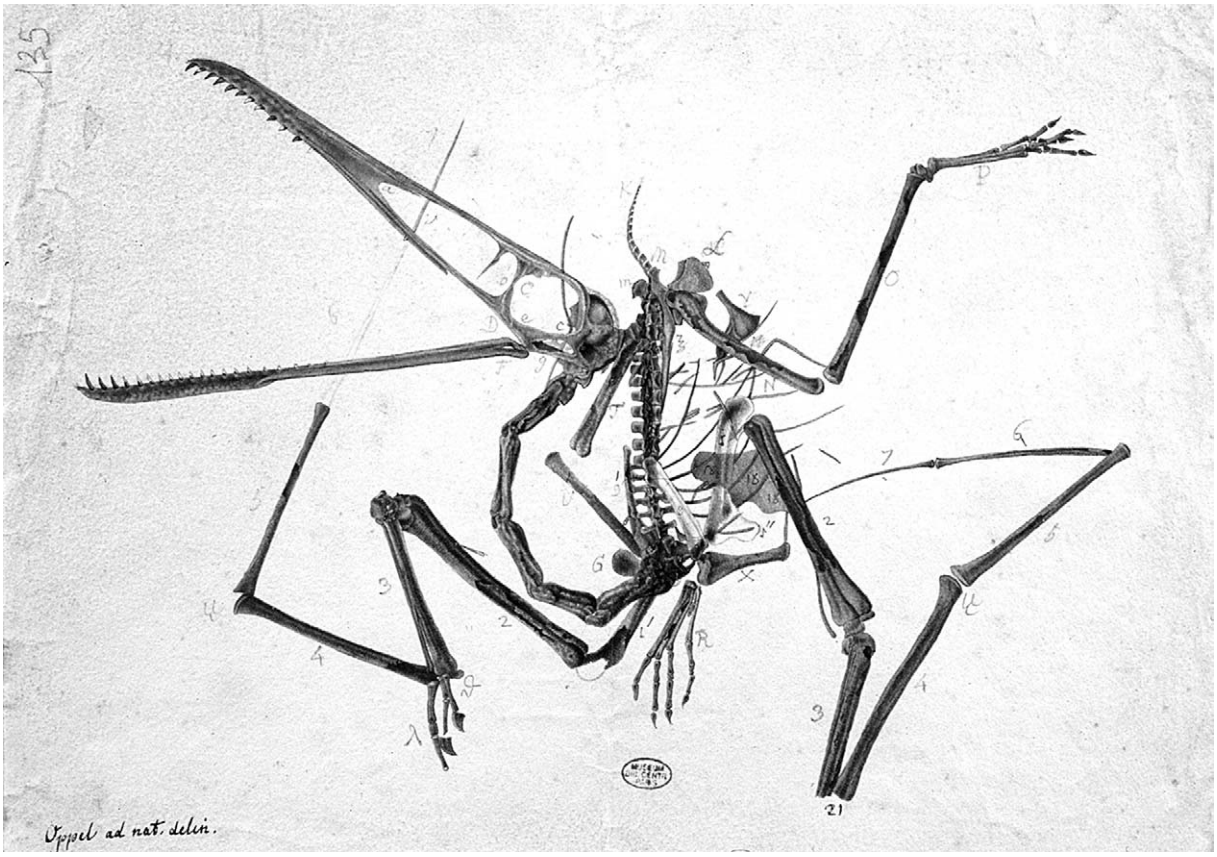

Fig. 4. Drawing of the pterodactyl made for Cuvier by Oppel (MS 629V, f° 135). Photo: MNHN, Paris, France.
Fig. 4. Dessin du ptérodactyle réalisé pour Cuvier par Oppel (MS 629V, f° 135). Photo : MNHN, Paris.

thicknesses of the long bones of the elongated finger are equal in thickness to four of those of the free fingers. In all these respects, Soemmerring said, the new find was just like *Ornithocephalus antiquus*; but the differences in the neck and the skull led him to erect a new species, *O. brevirostris*. (These remarks show that Soemmerring disregarded the arguments of Cuvier's 1809 and 1812 works, even long after he had received them.) With all this evidence in hand, Cuvier was able to form his decisive opinions on the animal, which were fully expressed in the second edition of *Ossemens Fossiles* in 1824, in thirteen pages of detailed criticism of Soemmerring's conclusions. He no longer had to defer, even formally, to Soemmerring's experience with the animal; he had the published descriptions and drawings of Collini and Soemmerring, he had illustrations from Oppel and Prévost, and he had the cast of the specimen itself.

7. Conclusions

The discovery of the earliest known restoration of a pterosaur, sent by Hermann to Cuvier in 1800, is of minor historical interest. It is, of course, fascinating and amusing, but it had no scientific or popular influence because it was never published. And it had no influence on Cuvier's views: he did not accept Hermann's opinion that the animal was a link between mammals and birds, nor that it had a hairy covering, because he noted specifically in *Ossemens Fossiles* [9] that because its bony features revealed its 'saurian' identity, it would accordingly have had reptilian soft parts, including scales (and 'generative organs', again in contrast to Hermann's restoration). On the other hand, Cuvier could only draw these conclusions because Hermann's letter had alerted him to the existence of the specimen that Collini had described. As soon as

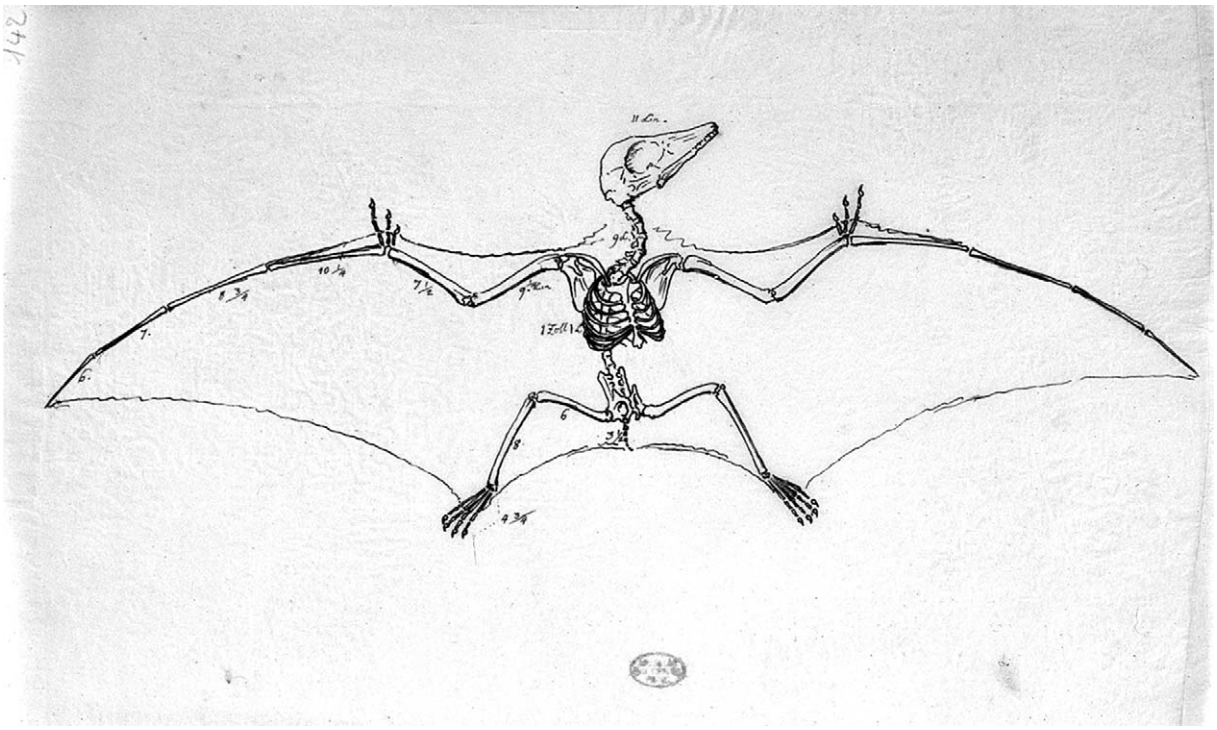

Fig. 5. The earliest known published restoration of a pterosaur, by Soemmerring (1817) [29]. Most soft parts are not restored, but the wing outline, for which the fossil provided no evidence, is distinctly bat-like (Ms 629V. f°142). Photo: Bibliothèque centrale MNHN, Paris, France.
Fig. 5. La première reconstitution connue d'un ptérosaure, par Soemmerring (1817) [29]. La plupart des parties molles n'ont pas été reconstituées, mais le contour des ailes, pour lequel le fossile ne fournit pas d'évidence, est distinctement celui d'une chauve-souris (Ms 629V, f° 142). Photo : Bibliothèque centrale MNHN, Paris.

he learned of it, he obtained Collini's paper and determined for himself what the animal really was. Within months, he had also adapted many of Collini's philosophical arguments to support his proposal to the Institut de France to undertake a full and comprehensive study of the known remains of fossil quadrupeds. For these reasons, Hermann's letter was decisive for Cuvier's future research plans.

The episode of the ptéro-dactyle is also instructive in illuminating taxonomic practice in the late 18th and early 19th centuries. Fossil animals and plants were recognized as distinctly different from living forms, yet in some respects allied to them. Classification was based on 'affinity', not on genealogy, and so taxonomic practice seems to us more fluid or plastic than it is today. In his same letter of 1800, Hermann also drew Cuvier's attention to a work by Murr [18], alleging that in China there was an animal with "bat wings, a bird head, and a long tail" (Murr's drawing is reproduced in Fig. 6), as if to suggest to Cuvier that chimeras such as Collini's specimen were still alive today. Cuvier [8] scoffed: "this is a fanciful image; and even if it were real, it would have nothing to do with our animal." Features that reflected mode of life were commonly used to establish the affinities of fossil animals that were substantially different from living forms (as Collini, Hermann, and Blumenbach did in this instance). Sometimes, as Collini did, one simply had to throw up one's hands in defeat. But experienced anatomists such as Soemmerring and Cuvier were able to reason from specific features that enabled affinities to be drawn. In Soemmerring's case, the misidentification of some bones (e.g., the shoulder and forelimbs), coupled with a willingness to accept general *Gestalt* of features as anatomically decisive, led him to reinforce his identification of the specimen as a bat at every turn. Cuvier, in contrast, looked past the functional modifications, as Collini [4] had counseled, to unmask the reptilian features that showed him the animal's true plan of organization.

Fig. 6. Knowing that the animal of whose existence Hermann was alerting Cuvier was so strange as to be regarded as a chimera by many naturalists, Hermann also drew Cuvier's attention to a similarly strange flying animal that allegedly lived in China, and had been alluded to by Murr (1775) [18 (Pl. C, Fig. 4)]. This is Murr's illustration (see text); Cuvier was not convinced. Photo: Bibliothèque centrale MNHN, Paris, France.

Fig. 6. Sachant que l'animal sur l'existence duquel Hermann avait alerté Cuvier était si étrange qu'il était considéré comme une chimère par de nombreux naturalistes, Hermann avait aussi attiré l'attention de Cuvier sur un animal volant également étrange censé vivre en China, et auquel Murr (1775) [18 (Pl. C, Fig. 4)] avait fait allusion. La figure représente l'illustration de Murr (voir texte) ; Cuvier ne fut pas convaincu. Photo : Bibliothèque centrale MNHN, Paris.

There is finally the question of the uses of restorations and their influence on later work. Although Cuvier's opinion of the *ptéro-dactyle* as a reptile was decisive, he never restored either of the specimens that were known in his time. But that was not uncharacteristic. In fact, apart from a few lines that limned the silhouettes and some muscles of fossil mammals from the Paris Basin such as *Palaeotherium* and *Anoplotherium*, Cuvier almost never allowed the restoration of any non-skeletal features in his illustrations [23]. However, in the case of the *ptéro-dactyle* he seems to have been particularly resistant. He concluded its description in *Ossemens Fossiles* (1824): "Given these facts, we could draw it as it was in life; but the figure that one would obtain would be most extraordinary, and would seem, to those who have not followed this entire discussion, the product of a sick imagination rather than the ordinary forces of nature."

Soemmerring's restoration, in contrast, had a profound influence from the beginning on restorations of pterosaurs in England [21]: his sketch was reprinted by Buckland in the *Bridgewater Treatise* of 1836, in which Buckland also provided a scene of pterosaurs resting on cliffs in a position much like Soemmerring's illustration. From that point, the more or less bat-like configuration of the wings and limbs was repeated and elaborated in English and American literature throughout the 19th and most of the 20th centuries, despite no actual evidence of any wings in specimens from those countries, and despite published evidence of more narrow wings that were known from German specimens [21].

As for Cuvier, he characteristically remained devoted to what he regarded as the actual evidence, and restricted himself to the most conservative inferences that could be drawn from these data. So it is perhaps all the more striking that he described the *ptéro-dactyle* in *Ossemens Fossiles* (1834–1836) in the following words:

> Thus we have an animal whose osteology from the teeth to the ends of the claws shows all the classic characters of saurians; one could not doubt that it also had these characteristics in its covering and its soft parts, that it would have had such scales, circulation, generative organs, etc. But this was at the same time an animal provided with the means to fly, which in its way of progression must have used its forelimbs very little, if in fact it did not keep them folded all the time, but whose resting position would have been ordinarily on its hind feet, again like birds; so, like them, it must have held its neck erect and recurved backward so that its enormous head would not lose all equilibrium.

Cuvier's description bears little resemblance to the features of Hermann's sketch. Nevertheless, Cuvier was decidedly impressed by the exotic, chimeric characteristics of the *ptéro-dactyle*, and by the diversity of views that he received about it. He concluded his descriptions of pterosaurs in the 1824 edition of *Ossemens Fossiles* with the simple but definitive statement: "Of all the organisms whose ancient existence is revealed in this book, these are incontestably the most extraordinary, and if we saw them alive, would seem the strangest as compared to all living beings."

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